PERGAMON

Vision Research 42 (2002) 1307–1324

Vision Research

www.elsevier.com/locate/visres

The cyclopean eye in vision: the new and old data continue to hit you right between the eyes

Hiroshi Ono *, Alistair P. Mapp, Ian P. Howard

Department of Psychology, Centre for Vision Research, York University, 4700 Keele Street, Toronto, Ont., Canada

Received 7 February 2001; received in revised form 29 May 2001

Abstract

We argue against recent claims by Erkelens and van Ee (Vision Res., in press) and by Erkelens (Vision Res. 40 (2000) 2411) that "the concept of the cyclopean eye is ... always irrelevant as far as vision is concerned" (p. 2??) and that "perceived direction during monocular viewing is based on the signals of the viewing eye only" (p. 2411), respectively. In Experiment 1, we presented a pair of small lights on a visual axis and measured the absolute visual direction of the near light with reference to different parts of the face. The near light appeared in front of the bridge of the nose or very near it, contrary to what was expected from Erkelens and van Ee's claim that monocular stimuli are seen in their correct locations. In Experiment 2, we replicated Erkelens' experiments with measurements of phoria and analyses of eye movements. The results confirmed his finding that the cyclopean illusion occurred rarely in the monocular condition, but our phoria and eye movement data provided the basis for a very different interpretation. Our data show that the oculomotor signal in his particular monocular condition was considerably weaker than in his binocular condition; therefore, the rarity of the monocular cyclopean illusion is not surprising. Moreover, since both claims above are based on an overgeneralization of the results of Erkelens' study, neither claim is persuasive.

1. Introduction

The generally accepted view on how the inputs from our eyes are combined to yield a percept of the direction of objects with respect to ourselves has been challenged by Erkelens and van Ee (in press) and Erkelens (2000). To date, the literature has shown that the physical information of both eyes is combined in such a way that we perceive the directions of objects as though we were viewing the world from an imaginary eye (the cyclopean eye) positioned midway between our eyes. That is, the two eyes operate not as two separate organs but as two halves of a single organ (Hering, 1868/1977). Because any valid challenge to an accepted view in science signifies progress, the two claims described in the abstract offer an exciting possibility for advancements in visual science. Any such challenge should not be taken lightly, however, but should be subjected to careful scrutiny. In this paper we examine the two claims and argue that they are invalid and unwarranted. We contend that Erkelens and van Ee's claim is incorrect when visual direction is operationally defined, and the domain of the concept of the cyclopean eye is made explicit, and that Erkelens' claim is untenable when the differences between his binocular and monocular conditions are examined closely. We support our contentions with two experiments.

In Experiment 1, we explore and clarify two possible meanings of perceived direction and we examine how each meaning relates to Erkelens and van Ee (in press) claim. The two possible meanings are absolute and relative direction as discussed recently by Mapp and Ono (1999). Based on the results of this experiment and the visual direction literature, we argue that Erkelens and van Ee's claim applies to relative direction but not to absolute direction: we maintain that the concept of the cyclopean eye is necessary in dealing with absolute direction.

In Experiment 2, we explore an alternative interpretation of Erkelens (2000) finding that the cyclopean illusion (see Fig. 1) occurs less frequently under monocular viewing conditions than binocular conditions. Specifically, we show that with his stimulus configuration, the eye movement signal is weaker (smaller and slower) in his monocular condition than in his binocular condition, consistent with Erkelens and Regan (1986)

* Corresponding author. Fax: +1-416-736-5814.
E-mail address: hono@yorku.ca (H. Ono).

0042-6989/02/$ - see front matter
PII: S0042-6989(01)00281-4

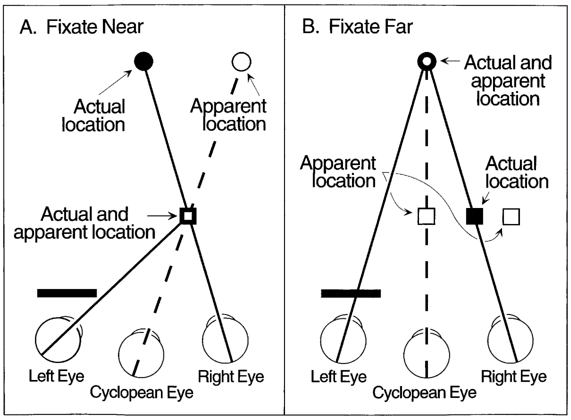

Fig. 1. Illustration of the cyclopean illusion as studied by Erkelens (2000). When fixation changes from the near stimulus (panel A) to the far stimulus (panel B) the absolute visual direction of the far stimulus shifts to the left. The two stimuli on the visual axis of the right eye are seen on the common axis (dashed lines). The near stimulus is seen as double when the far stimulus is fixated. The explanation of the illusion is that stimuli on the visual axis (or on a visual line) appear on the common axis (or on the cyclopean line) and that the location of the common axis (or the cyclopean line) changes with the change in binocular eye position. Note that the common axis is defined as a line passing through the intersection of the visual axes and the cyclopean eye, and therefore the concept of the cyclopean eye is needed in explaining the illusion.

finding that "as for the relative effectiveness of disparity (*binocular*) and accommodation (*monocular*) in driving ocular vergence, disparity has been shown to be considerably stronger" (p. 146; italics ours). The weak oculomotor signal is responsible, in part, for the difficulty in detecting the change in absolute direction in his particular monocular condition. We point out that his claim is based on a finding specific to his monocular condition and is incompatible with what is reported in the literature. We also point out that there is another factor that contributes to the difficulty in detecting the change in absolute direction in the monocular condition, namely, the relative direction of the stimulus with respect to the stable background remains constant.

Both experiments reported here are relevant to our two contentions, but Experiment 1 more directly addresses the issues raised by Erkelens and van Ee (in press) and Experiment 2, the issues raised by Erkelens (2000). Experiment 1 shows that two monocular stimuli on the visual axis of one eye (instead of one binocular and one monocular as shown in Fig. 1) appear on the common axis. That is, two monocular stimuli that are physically aligned with the viewing eye appear collinear, not with respect to that eye, but with respect to the cyclopean eye, and thus at least one of the two stimuli is seen in a non-veridical location. Experiment 2 replicates Erkelens' finding that only a minority of observers experience the cyclopean illusion in a monocular condition comparable to his. However, our measurement of the phoria associated with the stimuli and a more complete analysis of the eye movements provide the basis for a quite different interpretation.

2. Experiment 1: Demonstrating the distinction between absolute and relative directions

The basic phenomenon demonstrated is not new; Ptolemy (circa 100–170 AD) knew it (Howard & Wade, 1996). The phenomenon where stimuli on the visual axis of one eye appear on the common axis has been shown repeatedly throughout history. For example, Alhazen (1083/1989) showed it using lines on a board (see also Howard (1996)), Wells (1792) showed it using wires and string or two holes in a sheet of paper, and Hering (1879/1942) showed it as discussed shortly. In each of these examples, viewing was binocular and, therefore, binocular fusion of at least one stimulus and diplopia of a different stimulus were involved. In this experiment we show that this phenomenon is as robust under monocular viewing conditions, without fusion or diplopia, as it is under binocular conditions.

The critical stimulus in Experiment 1 was presented very close to the observer's face, thereby allowing for easy judgments of both its absolute and relative directions. Observers could report its absolute direction with reference to different parts of their face, for example, in front of their nose, between their eye and their nose, or in front of their eye, and they could also report its relative direction with respect to a more distant stimulus. In this experiment we presented two stimuli on the visual axis of one eye. We did this in six different viewing conditions in which, according to Erkelens and van Ee (in press), the critical stimulus should be seen directly in front of the eye. We had two viewing conditions that Erkelens (2000) did not have: the monocular stimuli were presented to each eye simultaneously without a binocular stimulus. According to their hypothesis, the critical stimulus for each eye in these conditions should also be seen directly in front of the eyes despite the fact that the two stimuli have the same horizontal local sign.

The purpose of this experiment is to (a) clarify the distinction between absolute and relative directions, (b) specify what inferences can and cannot be made on the basis of relative direction tasks, and (c) show that two targets collinear with one eye cannot be seen, simultaneously, in their veridical locations. These three aims are identical to those of Mapp and Ono (1999), who argued against Erkelens, Muijs, and van Ee (1996) claim that the cyclopean eye moves to the viewing eye. All of the arguments by Mapp and Ono apply equally to Erkelens and van Ee (in press), since their claim is the same as before with the exception that they do not use the term cyclopean eye. That is their claim, that with monocular viewing all stimuli on the visual axis (or visual line) are seen on that axis (or line), is identical to their claim that the cyclopean eye moved to the viewing eye. Hopefully, the inclusion of experimental evidence with our arguments in this paper will clarify this point. [1]

This experiment also addresses the following empirical question raised by Erkelens and van Ee (in press): What are the absolute visual directions of stimuli, collinear with one eye, when they are presented monocularly? This question is an important one, because Erkelens and van Ee's claim and Erkelens (2000) claim are based on the assumption that monocular stimuli are seen in their correct absolute directions, and answering this question should resolve the theoretical disagreement. Our understanding of Erkelens and van Ee's position is that they predict that monocular stimuli presented on a visual line of one eye would be seen on that line and aligned with that eye. Their idea is discussed in the context of Hering (1879/1942) classical demonstration in which a tree-top and a chimney (one on each visual axis) appear straight-ahead of the nose, while binocularly fixating on a spot on a window pane. According to their claim, these stimuli appear straight-ahead of the nose because of the averaging of two "vectors", one specified from each eye. When the stimuli are presented monocularly, however, there is no averaging and their prediction is that the tree-top or the chimney is no longer perceived straight-ahead of the nose (i.e., on the common axis), but rather they appear on the visual axis. As has been shown in the literature and as we will show again in Experiment 1, this prediction must be rejected.

2.1. Method

2.1.1. Observers

All 12 observers were naïve as to the purpose of the experiment. They ranged in age from 21 to 43 years. Six were unfamiliar with psychophysical or eye-movement experiments, but six had participated in many such experiments.

2.1.2. Stimuli and apparatus

The stimuli, similar to those used by Erkelens (2000), were four small light emitting diodes (LEDs) presented monocularly. Two of them, one for each eye, were presented approximately 2 cm from the cornea. The other two, again one for each eye, were positioned 30 cm from the observer's cornea. These four green LEDs (Chicago Miniature IDI 5370T5) were separated vertically so that the far right one was the highest followed by the far left, the near right, and the near left. Each LED was seen monocularly because of the arrangement of the four sheets of Polaroid filters as shown in Fig. 2. The observer could move the two far LEDs together in the frontal plane, inwardly or outwardly, by turning a knob. A pinhole pierced in a sheet of aluminum foil was placed in front of each near LED to reduce its angular size. The observer could move the near LEDs independently by turning two knobs attached to each of the LEDs. One knob moved the LED laterally (leftward or rightward) and the other moved it sagittally (forward or backward). The observer's head was stabilized with a biteboard.

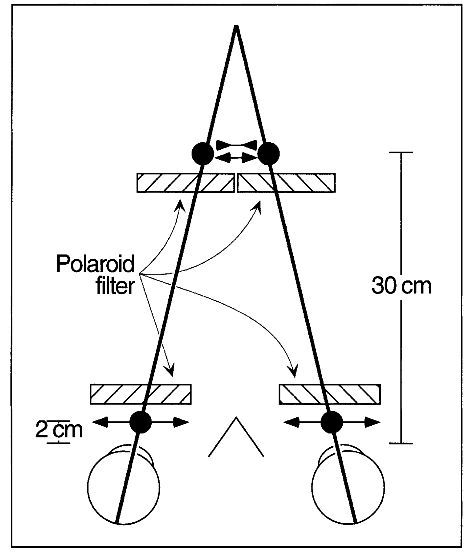

Fig. 2. Schematic drawing of the stimulus arrangement in Experiment 1. The bold arrows indicate the directions in which the stimuli could be moved. The near stimuli could also be moved forward and backward, but to simplify the figure this movement is not illustrated.

2.1.3. Pre-experimental procedure

The four LEDs were adjusted as follows. First, the experimenter positioned one of the near LEDs 2 cm in front of the observer's right eye, and confirmed that it could not be seen by the left eye. This was repeated for the near LED in front of the left eye. Second, the two far LEDs were turned on (one was seen by each eye) and the two near ones turned off. The observer turned the knob attached to the far LEDs until both were seen in the same horizontal direction. That is, one was seen above the other. Third, the pair of LEDs for one eye (one near and one far) was turned on, and the observer adjusted

[1] In this paper, we do not address Erkelens and van Ee (in press) argument against the use of the cyclopean eye concept when dealing with the visual directions of monocularly seen areas (Section 5 of their paper). A more complete description of Ohtsuka and Ono's (1998) hypothesis can be found in Ono, Ohtsuka, and Lillakas (1998), Mapp and Ono (1999), and Ono, Wade, and Lillakas (in press), and more empirical papers are in preparation. Readers are referred to these published papers to judge the merit of the hypothesis in contrast to the Erkelens and van Ee hypothesis.

the lateral position of the near one until the two appeared in the same horizontal direction. The same procedure was repeated for the pair of LEDs for the other eye.

2.1.4. Experimental procedure

Data were collected from each observer under each of three viewing conditions and two room light conditions. The three viewing conditions were (a) *double monocular*, in which both eyes were open and all four LEDs were presented, (b) *monocular with two eyes open*, in which only the pair of LEDs for the right eye or the pair for the left eye was presented, and (c) *monocular with one eye closed*, in which the pair for the right eye or the pair for the left eye was presented as in (b), but the eye to which the stimuli were not aligned was closed. The two room light conditions were (a) the *bright room* condition, in which parts of the apparatus such as the optic benches, the stimulus holders, and the wall behind the apparatus were visible, and (b) the *dark room* condition in which only the stimulus lights were visible. The six possible orders of presenting the three viewing conditions were combined with the two possible orders of room light conditions for 12 different observers. The three viewing conditions were presented as a block in the bright room condition and the dark room condition. For the first block, the pair of LEDs for the right eye and the pair for the left eye were presented in random order in viewing conditions (b) and (c). Before starting the second block, the alignments discussed in the pre-experimental procedure were checked, then the pair that was not used in the first block was presented.

After each stimulus presentation, the observers were asked to come off the biteboard and to report the relative direction of the near LED(s) with respect to the far one(s) (e.g., directly below the top one), and the absolute direction of the near LED(s) (e.g., in front of the nose, in front of the eye, or between the eye and the nose and by how much). In reporting the absolute direction, they were told to report where the near LED appeared to be located rather than where they knew it to be located. After reporting the two different visual directions, they were asked to get back on the biteboard and to close their eyes while the stimulus was changed for the next condition.

2.2. Results and discussion

The reported absolute direction of the near LEDs is presented in Table 1. The table clearly shows that the near LEDs were rarely seen in front of either eye, contrary to what was expected from Erkelens and van Ee (in press) claim. There were only two such reports out of the 72 reports made by the 12 observers. The most common report was that the near LED appeared either directly in front of the nose or very near the middle of the bridge of the nose. When the near LED was reported to appear close to the nose, the observer was asked to point to where it appeared on the face. All such observers pointed to a part of the bridge of their nose. Specifically, all 12 observers reported that the near LEDs appeared in front of the nose or near it in the double-monocular condition. The number of observers who reported "directly in front of the nose" decreased slightly in the other two conditions and the number of observers who reported "closer to the nose" increased.

As also indicated in Table 1, there were no systematic differences between the bright and the dark room conditions. (This lack of difference, especially in the one-eye-closed condition, is inconsistent with Erkelens (2000) hypothesis that the difference in luminance between the two eyes suppresses the oculomotor signals of the closed eye. See our footnote 5.) Therefore, we combined these two conditions before computing an index of where, on average, the near LED appeared (i.e., its absolute direction) across observers. We assigned the values 0, 1, 2, 3, and 4, to "in front of the nose", "close to the nose", "in between the nose and an eye", "closer to an eye", and "in front of an eye", respectively. For the double-monocular condition, we ignored the direction of deviation in the analysis. (For all but one of the observers that reported "close to the nose", the deviations were toward the left.) In the other two viewing conditions, we assigned positive values to deviations toward the viewing eye. There were no deviations toward the non-viewing eye. The computed means and

Table 1
Frequencies of absolute direction responses in the six conditions in Experiment 1

Monocular viewing condition	Absolute direction response categories in two room light conditions					
	Directly in front of the nose or (close to the nose)		In between the nose and an eye		Directly in front of an eye or (close to an eye)	
	Bright	Dark	Bright	Dark	Bright	Dark
Double	12 (4)	12 (6)	0	0	0	0
Two eyes open	12 (6)	11 (10)	0	0	0	1 (1)
One eye closed	10 (9)	10 (7)	0	1	2 (1)	1

(standard deviations) of these values across the different observers were 0.42 (0.42), 0.83 (0.49), and 1.17 (0.75) for the double, two-eyes-open, and one-eye-closed conditions, respectively. An analysis of variance for correlated observations showed that the differences between the conditions were statistically significant at $p = 0.006$, and a Tukey's (HSD) test indicated that the mean of the absolute direction in the double-monocular condition was significantly different from that of the one-eye-closed condition with $p < 0.01$.

Our finding, that several of the observers did not see the near LED precisely in the middle of the bridge of their nose in the double-monocular condition, reflects individual differences in the location of the cyclopean eye (e.g., Barbeito, 1981; Barbeito & Ono, 1979). The tendency for the near LED to appear deviated slightly toward the viewing eye in the two-eyes-open condition and in the one-eye-closed condition is probably related to an unequal weighting of the eyes (e.g., Banks, van Ee, & Backus, 1997; Barbeito & Simpson, 1991; Sheedy & Fry, 1979), since all such deviations were in the direction of the viewing eye. In the one-eye-closed condition, we think an additional factor is operating: the observers' knowledge of which eye is being used. We elaborate on the role of this knowledge in Section 4 because a deviation of approximately the same magnitude was found in Experiment 2. The point to be noted now, however, is that the near LED appearing slightly away from the horizontal center of the nose is not critical to our argument below. What is critical is that the near LEDs *rarely appeared in front of the viewing eye*, contrary to what is expected from Erkelens and van Ee (in press) claim. According to their claim the LEDs should have appeared directly in front of the viewing eye(s) in all three conditions.

Erkelens and van Ee (in press) assert that Hering (1879/1942) took an irrelevant step when he proposed that the vector defined by a visual target and its retinal image (i.e., the visual axis or visual line) translates to the cyclopean eye. It should be noted, however, that Hering's proposal does not involve a pure translation of vectors as suggested by Erkelens and van Ee. Our finding, which is consistent with Hering's demonstrations, shows that the vectors transfer to the cyclopean eye by rotating about the point at which they intersect the horizontal horopter that includes the intersection of the two visual axes. Examples of this rotation and transference, one for a visual axis and another for a visual line, are depicted in Fig. 3. The result of this rotation and transference is a "visual direction vector" and is the output of the visual system (a perceptual variable). The visual axes and visual lines, on the other hand, are the "input vectors" (physical variables) and should not be confused with the visual direction vectors. This description of how the visual direction vectors are determined from the inputs from the two eyes applies to both

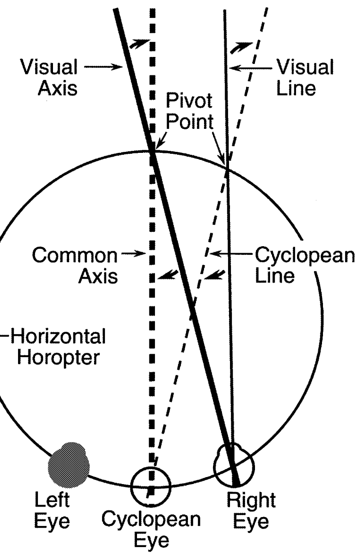

Fig. 3. An illustration of the rotation of a visual axis and a visual line about the point (labeled pivot point in the figure) at which they intersect with the horizontal horopter containing the intersection of the visual axes. To simplify the figure, the visual axis and the visual line of only the right eye are illustrated. For illustrations of this rotation and transference under binocular conditions, see Fig. 1 of Ono and Mapp (1995).

monocular and binocular stimuli and is consistent with van Ee, Banks, and Backus (1999) recent description.

The reported relative visual direction of the near LEDs with respect to the far LEDs was as follows. Both pairs of monocular LEDs (one pair to each eye) were reported to be in the same relative visual direction (i.e., one on top of the other) which is not surprising because each observer adjusted the near LED to appear this way in the pre-experimental procedure. Nonetheless, this result serves the purpose of distinguishing between absolute and relative visual directions. The results clearly show that inferences about absolute direction cannot be based solely upon the observers' reports of relative visual directions.

Our results concerning absolute and relative visual directions demonstrate that the direction of our near LED can be described in at least two ways. It can be described as appearing (a) in the same direction as (or toward the left eye or right eye) the subjective median plane of the head (i.e., in front of the nose), or (b) in the same direction as (or to the left or right of) the far LED. These two descriptions involve different reference axes, namely, (a) the subjective median plane of the head, for absolute direction, or (b) the direction of an arbitrary reference stimulus (the far LED), for relative direction. Asking observers to judge the direction of the near LED with respect to these two reference axes is the operational definition for each of the two types of visual direction. Asking about the absolute direction of the stimulus defines the domain in which the concept of the cyclopean eye is relevant. One of the difficulties in understanding the claims of Erkelens and van Ee (in press) or Erkelens (2000) is that they treat visual direction as a single construct, although a distinction between egocentric (absolute) and allocentric (relative) judgments is mentioned in Erkelens on p. 2411. Moreover, Erkelens and van Ee's conclusion that "a reference is *relevant* for motor tasks" but "it is *irrelevant* for visual direction tasks" (p. 9??) may account for the results of Ono, Wilkinson, Muter, and Mitson (1972) and Ono and Weber (1981) which used a pointing response with an unseen hand, but it fails to explain the results of the present study. There is no action involved with the near LED in this study, yet it appears in front of the nose.

Howard (1982, 1991) identified the sensory information required for each judgment. [2] Relative direction judgments require only information regarding the position of the object's retinal image(s), while absolute direction judgments require both retinal image information and information regarding the position of the eyes in the head. [Logically, an observer could process the absolute directions of two stimuli and derive the relative direction from them. This is not likely, however. See Brenner and Cornelissen (2000) and Sterken, Postma, de Haan, and Dingemans (1999).] Thus, when judging the relative direction of one stimulus with respect to another, be the stimuli monocular, binocular, or a combination of both, information regarding the position of the eyes in the head, or the position of the subjective median plane of the head, is not required. For example, two monocular stimuli with the same horizontal (and different vertical) local sign, or which fall within the Vernier acuity limits of the viewing eye, will appear aligned, regardless of eye position. [3] Where the stimuli appear relative to the face (or where the line that passes through the two stimuli appears to point on the observer's face), however, is an entirely separate empirical question.

Moreover, Howard (1982, 1991) analyses together with the results of Experiment 1 define the domains in which the concept of the cyclopean eye is and is not relevant. Clearly, the concept is not relevant for relative direction judgments, since these judgments require only information regarding "the position of the object's retinal image(s)". A rifleman's task is a good case to illustrate the domains. Consider a rifleman trying to align or make collinear a target, the front sight, and the rear sight. For the target to be hit, the absolute visual direction does not matter. What matters is the physical collinearity of the three points, the two sights and the target, which can be attained using a Vernier (relative visual direction) judgment (and consideration of the physical trajectory of the bullet). This does not mean, however, that there is no perceptual consequence. The perceptual consequence is illustrated in Fig. 4. Also see

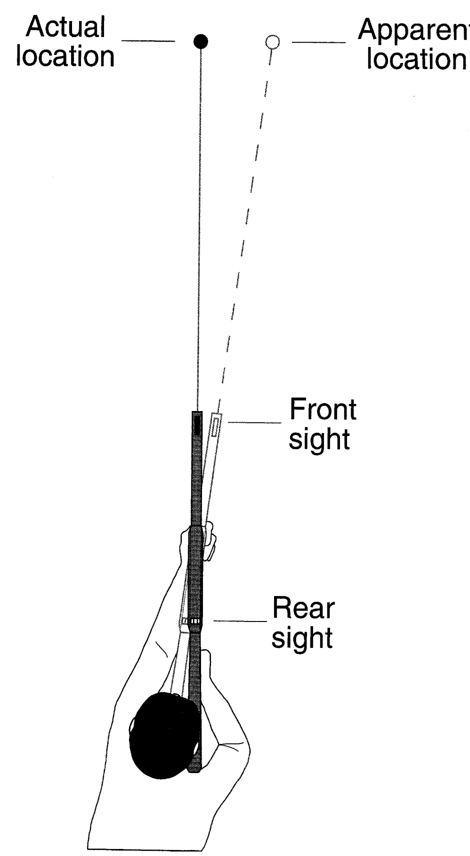

Fig. 4. The actual and apparent (absolute) visual direction of a target with respect to a rifleman who has monocularly aligned the target, the front sight, and the rear sight. In this task, not only is the concept of the cyclopean eye, "irrelevant", so too is the absolute direction of the target. The absolute visual direction of the target is inaccurate, but it does not matter for the question of whether the target is going to be hit or not. The figure is drawn as though the rifleman is esophoric when s/he accommodates to the front sight. If s/he is exophoric, the apparent location of the target would be on the left side of the actual target. If s/he has no phoria and the front sight is accommodated, the absolute visual direction of the target is still inaccurate just as the absolute visual direction of the tree-top and the chimney in Hering's demonstration are inaccurate. The front sight is analogous to the marker on the window pane and the target is analogous to the tree-top or the chimney in Hering's demonstration.

[2] What we refer to in this paper as absolute and relative directions were referred to as headcentric and oculocentric directions, respectively by Howard (1982). We chose to use the term "relative", rather than "oculocentric" to avoid the implication that the cyclopean eye is located in an eye. We chose the term "absolute", rather than "headcentric" so as to parallel and contrast the term "relative". The terms, absolute and relative, were also used in Mapp and Ono (1999) for the same reason.

[3] This assertion should be limited to two point-like stimuli. Recently, evidence is accumulating that, if monocular stimuli with the same horizontal (and different vertical) local sign are embedded in two different surfaces at different distances, they may not appear to be aligned. See for examples, Ono (1991), Erkelens and van Ee (1997), Popple and Findlay (1998), Shimono, Ono, Saida, and Mapp (1998), and Ono, Shimono, Saida, and Ujike (2000).

Fig. 4 of Ono and Barbeito (1982). Explaining what the rifleman is doing does not require the concept of the cyclopean eye, but explaining the perception illustrated in Fig. 4 (or what is found in Experiment 1) renders the concept necessary.

Note that in Fig. 4 (and Fig. 1) when the two stimuli on a visual line of one eye are physically collinear with respect to that eye, they are perceptually collinear with respect to the midpoint between the eyes. Therefore, the two LEDs at different distances on the visual line of one eye in Experiment 1 cannot both be seen simultaneously in their veridical physical locations as claimed by Erkelens and van Ee (in press) and Erkelens et al. (1996). In our experiment, the near LED, which was physically positioned directly in front of one eye, appeared non-veridically in front of the nose and perceptually collinear with respect to the far LED and the cyclopean eye. This was true for both the bright and the dark conditions. Thus, when describing the results of a visual direction experiment, confusions may arise if the distinction between physical (actual) location and perceptual (apparent) location is not made explicit. See p. 1 of Hering (1879/1942) and Mapp and Ono (1999) for an elaboration on this point.

The distinction between physical and perceptual location is also required to describe the empirical finding, of long standing, that what is on a visual axis (or a visual line) appears on the common axis (or a cyclopean line). Although this distinction is mentioned in Erkelens and van Ee (in press), it is not incorporated consistently. Two examples follow:

1. They state that, "Howard and Templeton (1966) and Mitson, Ono, and Barbeito (1976) would have been forced to conclude that the cyclopean eye is located in the sighting eye if they would have used their visual task in monocular viewing conditions." (p. 5??). The method involves adjusting a point to appear collinear with respect to another point and the "self", and Erkelens and van Ee are correct in suggesting that the line passing through the two stimulus points would physically point to the viewing eye. The long-standing empirical finding would tell us, however, that the line would appear to point to the bridge of the nose.

2. In their footnote 3 and Fig. 3 they claim that Alhazen (1083/1989) demonstration using lines on a board is "misleading" since having "the line point to the pupil of an eye" would lead to view "the two lines as dots". We are unclear as to what is misleading, but if the lines were to appear as dots they would fuse and would appear on the common axis as shown by Wells (1792) using holes in a sheet of paper that are aligned with the visual axis of each eye. They further state that "the retinal images are vertical lines instead of dots". If these two retinal images were seen as a (fused) vertical line in the median plane instead of a line pointing to the nose, then this would not be a compelling demonstration of the fact that stimuli on the visual axes appear on the common axis. [4] That is, the effectiveness of the demonstration depends upon the points on the vertical plane that contains the visual axis appearing at different distances. The seen lines in this demonstration clearly appear to hit you right between the eyes.

Although our Experiment 1 clearly shows that absolute visual direction is referred to the cyclopean eye, it does not provide an answer as to why the cyclopean illusion (Fig. 1) occurred infrequently in Erkelens (2000) monocular conditions. As he claims, the prediction from the principles of visual direction that the imaginary line passing through the two stimuli should appear to pivot at the cyclopean eye clearly failed in his monocular condition, except for 33% of his observers in the dark. It must be mentioned, however, that the extent of the cyclopean illusion in binocular and monocular conditions would not be equal unless the common axis, which is yoked to the intersection of the visual axes, moved through the same extent in *both* conditions. Our explanation of why the cyclopean illusion occurred infrequently in his monocular condition is based on two factors. First, given that accommodation (monocular) drives eye movements less effectively than disparity (binocular) it is unlikely that the common axis moved through as great an extent in his monocular condition as in his binocular condition. Second, it is likely that the presence of a stable background and the lack of change in the relative direction of his two stimuli "overrode" the small change in absolute direction. We discuss the second factor in Section 4 in reference to the results of his Experiment 3.

Our argument that the common axis moved through a lesser extent in Erkelens (2000) monocular condition than in his binocular condition is based on the following findings. Ono and Gonda (1978) and Ono and Weber (1981) found that absolute direction seen with one eye can be explained by the deviation of the common axis from the stimulus, namely, phoria. [Phoria is defined as "The direction or orientation of one eye, ... in relation to the other eye, manifested in the absence of an

[4] An experimenter dealing with only a single stimulus or stimuli on a given frontal plane need not invoke the concept of the cyclopean eye to describe the actual and perceptual positions of these stimuli. Furthermore, the concept of the direction need not be involved to describe the data: Cartesian coordinates to describe the positions on that plane are sufficient. Therefore, neither of these stimulus situations are ideal for discussions of the usefulness of the concept of the cyclopean eye. Erkelens and van Ee (in press) discussion in their Section 4 deals with these exact stimulus situations (perceptual displacement created with prisms), and the validity of their argument is hard to assess. When the experimenter deals with stimuli at different distances, however, the concept of direction and that of the cyclopean eye become apropos and necessary. We do not address this point further in this paper, except to refer readers to the comprehensive reviews of the topic in the chapter entitled "Adaptation to discordant stimulation" in Howard (1982) and "Adaptation of space perception" in Welch (1986).

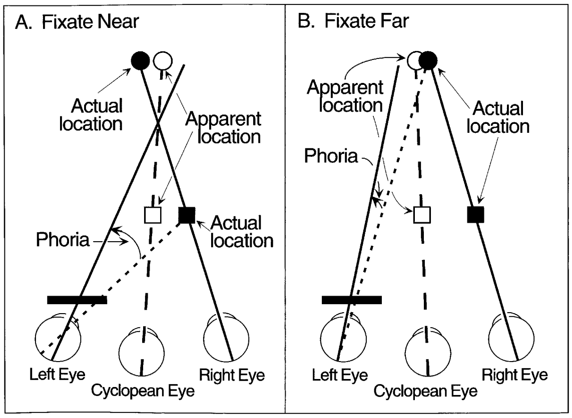

Fig. 5. Illustration of the apparent locations of stimuli on the visual axis of the right eye as a result of exophoria. The phoria is indicated by the angle between the visual line to the stimulus (dotted line) and the visual axis of the left eye. When fixation changes from the near stimulus (panel A) to the far stimulus (panel B) the absolute visual direction of the far stimulus shifts to the left. The two stimuli on the visual axis of the right eye are seen on the common axis (dashed lines) as in Fig. 1, but the motion of the common axis as a function of the change in fixation is smaller.

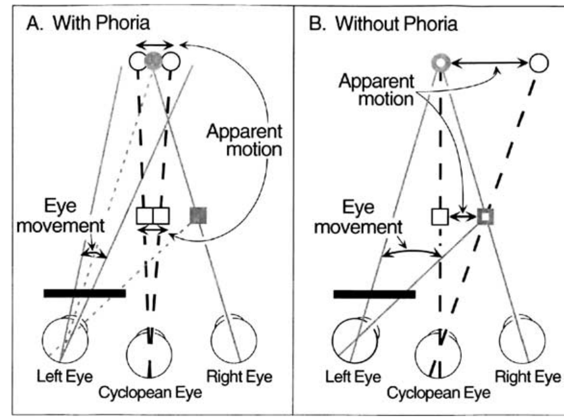

Fig. 6. Illustration of a reduction in the extent of the cyclopean illusion as a result of phoria. The extent of the apparent motion of the common axis with phoria (panel A) is derived from the two fixation conditions shown in Fig. 5. The extent of the apparent motion of the common axis without phoria (panel B) is derived from the two fixation conditions shown in Fig. 1. The extent of apparent motion is smaller with phoria than without.

adequate fusion stimulus ..." (p. 529, Cline, Hofstetter, & Griffin, 1989). See Fig. 5 for an illustration of phoria.] Others have found that the magnitude of phoria, with respect to the fixation point, increases with closer fixation (Holland, 1958; Ono & Weber, 1981; Barbeito & Simpson, 1991). If one thinks of phoria as a mismatch between accommodation and vergence angle, then our argument can be understood by considering the effectiveness of accommodation in an accommodative vergence situation. First, consider the case in which accommodation is completely ineffective, such as when the stimuli are closer than the eye's near point of accommodation. In this case, the occluded eye would drift to the physiological resting state (for a discussion, see e.g., Owens and Tyrrell (1992)), and would remain there. Second, consider the case in which accommodation is effective but the coupling between accommodation and vergence is not perfect, and in which exophoria is larger when the stimulus is closer. Such a case is illustrated in Fig. 5 in which panel A shows larger exophoria than panel B. In this case, the common axis would move through a lesser extent than in a binocular condition. Finally, consider the case in which accommodation is effective and the coupling between accommodation and vergence is perfect. In this case, the occluded eye would move in accordance with the change in accommodation, and the common axis would move through the same extent as in a binocular condition.

From the different extents of eye movements (and common axis movement) described in the three monocular situations above we predict different extents of the cyclopean illusion. No illusion is predicted for the condition in which accommodation is ineffective, because the common axis does not move. The extent of the illusion for the condition in which accommodation is partially effective is illustrated in panel A of Fig. 6. The extent of the illusion predicted in the condition in which there is no phoria is illustrated in panel B of Fig. 6. (The extent of the illusion in panel A is derived from what is illustrated in Fig. 1.) Note that the extent of the illusion is smaller in panel A, which depicts the usual monocular condition, than in panel B, which depicts the unusual monocular condition in which the extent of the eye movement is the same as it would be in a binocular condition. Phoria also accounts for the two informal observations reported by Erkelens (2000). His Observation 1 (pp. 2412–2413), that a bead moving toward the eye along the visual axis appears "as a pure approach without any change in direction", can be explained by the phoria increasing as the bead approaches. Furthermore, the first part of his Observation 2 (p. 2413) that there is an apparent shift in the absolute direction of a stimulus positioned straight-ahead of the nose, when binocular viewing is switched to monocular viewing, can also be explained by the phoria that takes place. Moreover, his observation that the magnitude of this apparent shift increases as the viewing distance decreases is completely consistent with the phoria literature—namely, the smaller the viewing distance the greater the exophoria. In the second part of Observation 2, Erkelens noted that there is no such apparent shift, when a portion of the stimulus on the same sheet of paper is occluded. This can be explained by a lack of phoria, because phoria does not occur when a binocular stimulus is present. Irrespective of whether phoria occurs or not, his Observation 2 does not provide any evidence in support of his claim that "perceived direction during monocular viewing is based on the signals of the viewing eye only" (p. 2411). If anything, this observation contradicts his claim. That is, when one closes one eye in this situation the open eye remains directed at the target and the image of the target remains on the fovea. Therefore, if the visual system were to switch from monitoring the signals of both eyes to monitoring the signals of the viewing eye only there would be no shift in the absolute direction of the target. Moreover, even if the open eye were to move, the movement of the eye would be accompanied by an equal and opposite shift in the angular position of the target's retinal image, and again there would be no shift in the absolute direction of the target. In any event, his Observations 1 and 2 do not constitute grounds to dismiss, as he has done, the previously published reports about the monocular cyclopean illusion that he cites (i.e., Ono et al., 1972; Ono & Gonda, 1978; Ono & Weber, 1981; Park & Shebilske, 1991).

3. Experiment 2: Redoing of the dark condition of Erkelens' Experiment 2 with measurements of phoria and eye movements

Before introducing Experiment 2, we comment on the eye-movement traces (p. 2416) in Erkelens (2000) binocular and monocular conditions. We disagree with Erkelens' claim that the eye movements in the two conditions are essentially the same. Our inspection of his Fig. 3 indicates that (a) both the "tracking" and "stepping" eye movements in his monocular conditions are smaller than in their respective binocular conditions, which is consistent with the idea that the closer the stimulus the greater the phoria, and (b) the "stepping" eye movements in his monocular condition are slower than in the binocular condition (i.e., the destination is reached by a slow asymmetrical vergence in his monocular condition, whereas it is reached by fast binocular saccades in his binocular condition). The conclusion from our inspection of his tracking data is consistent with Erkelens and Regan (1986) finding that a monocular stimulus is considerably less effective at driving an eye movement than is a binocular stimulus. Moreover, the conclusion from our inspection of his stepping data is consistent with the literature pertaining to accommodative vergence eye movements in response to a stepped stimulus (e.g., Alpern & Ellen, 1956; Hermann & Samson, 1967; Keller & Robinson, 1972; Kenyon, Ciuffreda, & Stark, 1978; Ono & Nakamizo, 1978; Cumming & Judge, 1986; Enright, 1992; Saida, Ono, & Mapp, 2001) and with reports about binocular fixation changes between stimuli on a visual axis (e.g., Alpern & Ellen, 1956; Westheimer & Mitchell, 1956; Riggs & Niehl, 1960; Yarbus, 1967; Ono & Nakamizo, 1977, 1978; Ono, Nakamizo, & Steinbach, 1978). The differences we note between Erkelens' monocular and binocular conditions are well documented in these references. Therefore, it is very likely that the smaller and slower eye movements in his monocular conditions contributed to his observers not experiencing the cyclopean illusion. Moreover, individual differences in the magnitude and the angular velocity of eye movements may account for why 33% of his observers did experience the cyclopean illusion in the dark.

Experiment 2 had four parts. In part (a) we measured the relative visual direction of monocularly presented stimuli comparable to those used by Erkelens (2000) with respect to the absolute direction of the near LED used in Experiment 1. In part (b) we determined the number of observers who experience the cyclopean illusion. In part (c) we measured the phoria associated with the stimuli. In part (d) we measured and analyzed the eye movements of several observers. Comparable to Erkelens' tracking condition, our observers tracked a stimulus that moved back and forth on the visual axis of one eye; comparable to his stepping condition, our observers changed fixation between two stationary stimuli positioned on the visual axis of one eye. For (a) and (b) we presented these two conditions with the near LEDs used in Experiment 1. For (c), we measured phoria at the end of the experiment, and for (d), we asked several observers to return to have their eye movements recorded.

3.1. Method

3.1.1. Observers

The observers who served in Experiment 1 participated in parts (a)–(c) of Experiment 2. There was a rest period of approximately 10 min between the two experiments. Four observers from the original 12 participated in the portion of the experiment to measure eye movements. Two of them had reported the cyclopean illusion and two had not. The eye movement recording sessions took place three or four weeks later.

3.1.2. Apparatus and stimuli

Two additional LEDs (Chicago Miniature IDI 5370T7) which emitted yellow light instead of green light replaced the far LEDs in the apparatus used in Experiment 1. They were mounted on a moveable track such that they could be aligned with the right eye and also to the near (green) LED used for the right eye in Experiment 1. The biteboard and the near LED were positioned as in Experiment 1. Phoria was measured by placing a variable diopter prism, with a range of ± 30 diopters and Maddox rods, in front of the left eye. The measurement involved adjusting the variable diopter prism until the image of a light source that appeared as a vertical line of light (produced by the Maddox rod over the left eye) appeared superimposed on the light source seen from the right eye. The extent of the adjustment defined the phoria.

The eye-movement recording sessions were conducted in a different room, and the near LED was removed because it interfered with the eye-movement recording system. Except for this, the stimulus configuration was the same and the moving LED was moved with a MFE (model no. 835M) X–Y Plotter, instead of having it moved manually by the experimenter. Horizontal eye movements were recorded with the El-Mar Series 2020 binocular CCD video-based eye tracker, which has high resolution and compares favorably to the magnetic search coil technique (DiScenna, Das, Zivotofsky, Seidman, & Leigh, 1995). The system has a maximum resolution of 6 min of arc, a 120 Hz sampling rate and a linear range of $\pm30°$ and $\pm25°$, in the horizontal and vertical meridia, respectively.

3.1.3. Procedure

The basic experimental design for parts (a) and (b) consisted of the two eye-movement conditions mentioned above. In the tracking condition, the experimenter moved the closer yellow LED back and forth 10 times through a 13 cm extent from 15 to 28 cm as smoothly as possible with a cycle of 3 s. A metronome set to sound every 1.5 s was used to synchronize the movements. (Before each experimental session, the experimenter practiced moving the LED.) In the stepping condition, observers were instructed to alternately change their fixation 10 times between the two yellow LEDs (at their own pace). One LED was 15 cm and other was 30 cm in front of the observer's eye. An eye patch was placed over the left eye. For half of the 12 observers the tracking condition preceded the stepping condition, and for the other half the stepping condition preceded the tracking condition.

After each stimulus presentation, observers were asked three questions: (a) To which part of your face did the imaginary line, connecting all three lights, appear to point? (b) As you tracked the near yellow light or as you changed fixation between the two yellow lights did the imaginary line appear to shift? If so, how? (c) Relative to your face, where did you see the green light? (i.e., in front of your nose, in front of your eye, or in-between your nose and your eye). After reporting their percepts, they were asked to close their eyes while the stimulus was adjusted for the next condition.

Following the two stimulus presentations, phoria was measured for the two LEDs that were 15 and 30 cm away from the observer (as in the stepping condition). There were three measurements for each distance. In the eye-movement session, before data collection for each observer began, the recording system was calibrated by having fixations at seven vertical and seven horizontal points across a range of $\pm10°$ at a distance of 2 m from a calibration array projected onto a screen.

Eye movements were recorded for binocular as well as monocular conditions in the bright and dark room conditions. The eye-movement recording portion of the experiment had eight conditions ($2 \times 2 \times 2$), namely, tracking and stepping $\times$ binocular and monocular $\times$ bright and dark room illumination conditions. Within each of these conditions we recorded the observer's eye movements for a period of 1 min. In the tracking condition this represented 20 cycles and in the stepping condition (which was self-paced) it represented 10–23 cycles. The "binocular" refers to the near stimulus being binocular but not the far one (see Fig. 1). For the monocular condition, the patch over the left eye was replaced by an occluder positioned behind the camera.

3.2. Results and discussion

Most observers reported that the imaginary line connecting the three LEDs pointed to the nose or near it, and that the near one appeared in front of or near the nose. However, the two reports were not always consistent. One observer reported that the line pointed to the right eye in both the tracking and stepping conditions, but reported that the near LED appeared near the nose in the tracking condition and near the eye in the stepping condition. This observer was the one who reported that the near LED appeared in front of an eye in Experiment 1. We performed the same analysis as in Experiment 1 to summarize where on the face the line appeared to point or where the near LED appeared with respect to the face (i.e., the absolute direction). The means and (standard deviations) were 1.13 (1.11) in the tracking condition, and 1.17 (1.25) in the stepping condition. The numerical values are close to those obtained in the one-eye-closed condition in Experiment 1 and are discussed in Section 4. Note that, except for the one observer reported above, both the stationary and the moving LEDs were referred to the cyclopean eye. Therefore, the rarity of the monocular cyclopean illusion noted by Erkelens (2000) is not a consequence of the directions of the LEDs being referred to the viewing eye.

Four observers reported apparent movement of the imaginary line, but only two reported what we would consider to be the cyclopean illusion. Observer LT reported that the line pivoted very near the face and the far stimulus moved about 1.5 cm in both the tracking and the stepping conditions. Observer YL reported the same perception but only in the tracking condition. Observer CL reported that the line pivoted very slightly at the far LED and the near green one appeared to move slightly in the tracking condition; TR reported the same in the stepping condition. We have no good explanation for this report, except to speculate that the procedure for

Table 2
Phoria in diopters for two distances for each observer and the occurrence of the cyclopean illusion in Experiment 2

Observers	15 cm	30 cm	Illusion
RK	30.00+	9.00	No
LT	5.13	0.88	Yes
NT	21.00	−11.67	No
LL	30.00+	7.33	No
PG[a]	8.60	−5.00	No
CA	27.25	7.00	No
CL	30.00+	11.00	No
DH	27.33	4.67	No
MK	30.00+	10.00	No
YL	30.00+	2.67	Yes[b]
DT	30.00+	12.00	No
TR	30.00+	18.67	No
Mean	?	5.55	
SD	?	8.08	

[a] PG was able to superimpose the LED and the apparent line by changing his vergence. His phoria values were obtained by asking him to view the stimuli "passively".
[b] In one condition.

aligning the three LEDs was inadequate for these two observers. [5]

The means of the phoria in diopters for each observer are shown in Table 2. (One prism diopter corresponds to a 1 cm displacement of the light at a distance of 1 m.) Also, the two observers who experienced the cyclopean illusion are identified in the table. For all 12 observers, the phoria at 15 cm was considerably larger than at 30 cm. Indeed, for seven observers, the phoria at 15 cm was larger than we could measure with the ±30 diopter variable prism. The very large phoria associated with the near LED (15 cm) indicates that, when fixating at this distance in either the tracking or the stepping condition, the visual axes intersected at a point far beyond the stimulus. Given that this was likely the case in Erkelens (2000) study, the extent of the eye movements in his monocular condition would be much smaller than in his binocular condition. Note that the two observers who experienced the cyclopean illusion had the smallest phoria for the stimulus at 30 cm. The results shown in Table 2 strongly suggest that the weaker oculomotor signal was a contributing factor in the low frequency of seeing the cyclopean illusion in the monocular condition.

There is, however, another logically feasible way to describe this weakness. All eye movements, including those with one eye held stationary, can be formally analyzed in two ways. One way is to describe the movement of each eye separately, another is to describe the movements of both eyes as consisting of two components, namely, version and vergence. In the second description, the relevant oculomotor signal for absolute visual direction is the version signal. (For a more elaborate discussion, see Howard (1982), Ono (1980, 1983).) To explain the difference between the binocular and monocular conditions in Erkelens (2000) study, we analyzed the eye movements of four observers in terms of the version component derived from their eye movements (the mean magnitude and the mean peak angular velocity). In this experiment, the predicted magnitude of the version component when there is no phoria or fixation disparity is 5.33° in the tracking condition (the stimulus moved only to 28 cm), and 5.76° in the stepping condition. (These magnitudes were calculated using the value of 6.2 cm for the interocular distance.) A larger version component than the predicted value is expected in the binocular stepping condition because, in this condition, the far stimulus was monocular and, therefore, when the observer attempts to fixate it the visual axes would intersect beyond and to the left of the stimulus due to exophoria.

The mean magnitudes of the version component of the eye movements in both the tracking and the stepping condition, and the mean peak angular velocity in the stepping condition are shown in Fig. 7. The mean values for the stepping conditions are based on the data from three observers only. Observer YL was unable to move her eyes in the two stepping conditions. See Appendix A for her sample eye movements. The figure shows two striking differences that are not reported in Erkelens (2000): (a) the monocular condition produced much smaller and slower eye movements than the binocular condition, and (b) within the monocular condition, the dark condition produced smaller and slower eye movements than the bright condition. The difference described above in (b) suggests that in the bright condition an isotropic rate of change in retinal image size of the stimulus holder served as a cue for a change in the distance (e.g., for perception, see Gray and Regan (1998), Ittelson (1951), and Regan and Beverley (1978); for eye movement, see Erkelens and Regan (1986)), and that in the dark condition a small LED as a fixation point is a poor stimulus for accommodation (Aggarwala, Nowbotsing, & Kruger, 1995; Owens & Leibowitz, 1975). In Appendix A, we show sample eye-movement traces of all four observers, with the mean and standard deviation of the magnitude of the eye movements for each subcondition, to comment on the individual differences in the eye movements and on Erkelens' own eye movements.

The mean magnitudes and the mean peak angular velocities of the eye movements shown in Fig. 7 clearly contradict Erkelens' (2000) interpretation of his data that, "In general, the amplitudes and the speeds of the eye movements were similar in binocular and monocular viewing conditions." (p. 2415). Our data show that the monocular condition produces smaller and slower eye

[5] When preparing our Addendum we realized that this speculation is incorrect.

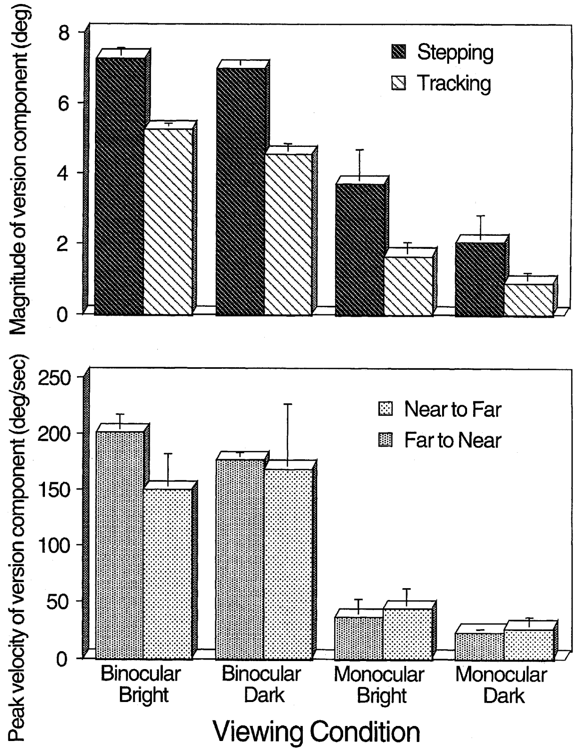

Fig. 7. Histograms showing the mean magnitudes and peak angular velocities of the version component of the eye movements from the four observers who participated in the eye-movement monitoring session in Experiment 2. The upper panel shows the mean magnitude and standard error in the tracking and stepping conditions. The lower panel shows the mean peak angular velocity (absolute values) and standard error of the near-to-far and far-to-near eye movements in the stepping condition ($n = 4$ in the tracking condition; $n = 3$ in the stepping condition).

movements than the binocular condition. Moreover, we think his data do, too, if he were to analyze them as we did ours. Our finding is consistent with the tracking eye movement data reported in Erkelens and Regan (1986) and with the stepping eye movement data reported in the literature cited in the preamble of this section. Thus, our finding and the literature cast into doubt Erkelens' assertion that, "The important conclusion from this result is that eye movements do not explain the absence of the cyclopean illusion during monocular viewing." (p. 2415). The smaller and slower eye movements partly account for why only a small number of observers experienced the cyclopean illusion in his and our monocular conditions. The data also show, however, that the eye movements or lack thereof are not the sole determining factor. This is so, because the monocular eye movements in the bright condition were larger than in the dark condition, yet none of the observers experienced the illusion in the bright condition in Erkelens' study. Another contributing factor is discussed in the next section with reference to his finding that, "None experienced the illusion during monocular viewing of monocular targets against a large background." (p. 2416). We speculate that this finding is due to the relative visual direction of a monocular target with respect to a stable background remaining the same despite a movement of the non-viewing eye.

This speculation indicates that Erkelens and van Ee (in press) assertion that "the argument that the two eyes always act as a single sensor was recently falsified by experiments ... (Erkelens, 2000)" (p. 4??) is at best premature. Moreover, their generalization that the cyclopean illusion does not occur "... during monocular viewing of full-field scenes in daylight conditions" may also be premature. First, the literature, without specifying the requirement of darkness, documents the existence of the illusion under monocular viewing conditions (e.g., Carpenter, 1988, pp. 308–309; Enright, 1988, p. 925; Helmholtz, 1910/1962, p. 253; Hering, 1879/1942, p. 42; Wells, 1792, p. 79). This suggests to us that the illusion is likely to occur in a daylight condition without a background (or with a background that does not provide any information about the relative direction of the target). Second, the phoria results of our experiment indicate that having the two accommodative stimuli very close to the face is not conducive to producing the illusion. Thus, unlike the stimulus arrangements chosen by other researchers, the particular arrangement used by Erkelens was one for which it is particularly difficult to produce a monocular cyclopean illusion. [6]

Since these possibly premature generalizations are the basis of the arguments in Erkelens (2000) and Erkelens and van Ee (in press), their arguments are not persuasive. The traditional view that the two eyes work as one organ (Hering, 1868/1977) is more parsimonious than Erkelens', in that no new mechanism is required. His idea requires that the visual system monitor the signals of the viewing eye only, when the stimulus is seen monocularly in the light and sometimes in the dark, and then switches to monitoring the signals of both eyes when there is a binocular stimulus. We find it difficult to imagine the advantage of his proposed mechanism or what kind of evolutionary pressure would create it, particularly because a monocular stimulus is not referred to the viewing eye as indicated in the literature and as we found in Experiment 1.

[6] We are now planning experiments to determine the necessary conditions for the monocular cyclopean illusion. In a pilot study, we changed the distance of the stimulus and asked observers from Experiment 2 that did not see the illusion to come back. Most of these observers now experience the illusion. In these experiments, we will test Erkelens (2000) hypothesis that when one closes one eye the resultant difference in luminance between the two eyes causes the signals of the closed eye to be suppressed.

4. General discussion

In our discussions of Experiments 1 and 2, we did not make a distinction between visual and motor reference points as did Erkelens and van Ee (in press). We have treated the two terms as synonyms and also as being synonymous with other terms such as binoculus, center of visual direction, and projection center. However, when clear operational definitions to distinguish between visual and motor reference points are provided, the distinction between them may eventually provide a better understanding of how the visual system processes direction. (For a discussion of operational definition see e.g., Bridgman (1927), Feigl (1945), Green (1992), and Stevens (1935).) Detailed experimental procedures to measure the construct are needed, as we have done for the distinction between absolute and relative directions in Experiment 1. Moreover, the motor reference point they propose must also be operationally distinguished from the kinaesthetic-tactile reference center discussed in Howard and Templeton (1966). The different methods (see e.g., Barbeito and Ono (1979), and Howard and Rogers (1995)) that have been used to measure the visual center may indeed be measuring different points that should be explained by different constructs, since reference points measured with different methods do not correlate across different observers (Mitson et al., 1976). None of the methods, however, indicate that the center is located in one eye as required by Erkelens et al. (1996) proposal, and the lack of correlation among different methods may be due to the lack of precision of these methods. In working towards better operational definitions of whatever construct may emerge to explain visual direction, the points made below must be incorporated.

Although the assumption in visual direction research is that absolute or relative direction is processed independently of depth or distance, the distance of the stimulus is an important experimental variable. For a very distant stimulus, visual direction referred to the cyclopean eye becomes experimentally indistinguishable from that referred to one eye. Our presenting the near stimuli very close to the eye(s) in Experiments 1 and 2 allowed us to make inferences about absolute direction. Erkelens (2000) presentation of the accommodative stimuli too close to the face led to a low frequency of observers experiencing the cyclopean illusion.

There is another subtle but important experimental variable that was not controlled for in either our study or Erkelens (2000), namely, the observers' knowledge of (a) where the stimuli are with respect to their face, (b) which eye is being used, and (c) where each eye is located in their head. If observers were to base their judgment solely on this knowledge, they would have to report that the near stimulus is in front of the viewing eye. Moreover, there can be a subjective impression that we are seeing with and from the viewing eye, analogous to the impression that observers get when performing an utrocular-discrimination task. (For discussions, see e.g., Blake and Cormack (1979), Ono and Barbeito (1985), and Steinbach, Howard, and Ono (1985).) For example, dropping an eye drop into an eye does not give an impression of dropping it on the bridge of the nose, nor does looking through a tube or a single view microscope give a compelling impression that we are seeing as though from the bridge of the nose. [7] The point being made is that the subjective impression that one is seeing from one eye is likely based on the knowledge listed above and is not necessarily counter evidence for the idea that we see as though from a cyclopean eye. An analogy is that the subjective impression of seeing with a particular eye does not indicate that one can make such a discrimination under controlled experimental conditions. We speculate that the knowledge listed above affected the observers' reports. The subjective impression that we are seeing from one eye is likely to have contributed to the report made by one observer in the one-eye-closed condition in Experiment 1, and in Experiment 2 in which an eye patch was used. In both experiments, he asked during the pre-experimental procedures whether to align the stimulus to an eye when we instructed him to move the stimulus to appear above or below another one. That is, he had the knowledge that the stimuli were being aligned to an eye. We further speculate that this knowledge played a role in the claims that the cyclopean eye moves to the viewing eye (Erkelens et al., 1996), that only the signals from the viewing eye are monitored (Erkelens, 2000), and that the cyclopean eye is always irrelevant (Erkelens & van Ee, in press).

There is nothing in our results or in the literature that supports Erkelens and van Ee (in press) claim that the cyclopean eye is always irrelevant, or Erkelens (2000) conclusion in his last paragraph that what is stated in Ono (1991) "is not correct". This is not to say, however, that the laws of visual direction as summarized in Ono (1991), in Ono and Mapp (1995), or in Howard and Rogers (1995) are complete enough to account for visual direction in all stimulus conditions. One thing that is missing is consideration of the background. For example, there is no provision in the laws to incorporate the Duncker effect (Duncker, 1929/1935) or induced movement (see e.g., Howard (1991), and Wade and Swanston (1987)). While fixating on a stationary dot surrounded

[7] Placing an index finger in front of an eye also does not lead to a perception that the finger is in front of the nose. Ono and Angus (1974) considered this stimulus situation as producing a conflict between the absolute visual direction and the felt position of the finger and performed an adaptation experiment. When the finger is repeatedly placed and removed from in front of the eye, the felt position of the finger changed in the direction of the nose as indicated by open-loop pointing to that finger with the index finger of the non-adapted hand.

by a moving background, the dot appears to move in the direction opposite the background and the background tends to appear stationary. This phenomenon is an example of what cannot be explained by the existing laws of visual direction. A more striking violation of the laws is the phenomenon in which an after-image of an entire room remains perceptually stationary even when the observer makes an active eye movement (Davies, 1973; Pelz & Hayhoe, 1995; Swindle, 1916; Zenkin & Petrov, 1979). These phenomena suggest to us that information about the relative direction of a stimulus, with respect to the background, can "override" the information about absolute direction information from the oculomotor signals and the retinal signals. The results of Erkelens' Experiment 3 reflect how large the background had to be before it had its effect on his four observers who experienced the cyclopean illusion (rather than how large the difference in luminance to the two eyes had to be). Moreover, the lack of the illusion in daylight in his monocular conditions can be attributed to the background remaining perceptually stationary, and to there being no change in the relative direction of the two stimuli or the moving stimulus, relative to the background in his Experiments 2 and 3.

The foregoing discussion also suggests that the visual system is more sensitive (indicated by a lower discrimination threshold) to relative direction than to absolute direction. "Hyperacuities" such as Vernier acuity are in the seconds of arc range, whereas the standard deviation of setting a stimulus at 25 or 50 cm to the subjective median plane is over 2° within and between observers (Ono & Weber, 1981). Moreover, when we attempted to measure the subjective straight-ahead by having observers set the position of a binocularly viewed single light 2 m away in the dark in a pilot study, we found that some observers did not see the movement of the light, even though the same movement was easily seen when the room lights were on in Ono, Tam, and McConnell (1983). The high precision for relative direction judgments and low precision for absolute direction judgments are consistent with the general psychophysical fact that relative judgments are more precise than absolute judgments. For example, a common or absolute motion is more difficult to detect than relative motion (e.g., Leibowitz, 1955; Snowden, 1992), and a change in absolute disparity is more difficult to detect than a change in relative disparity (e.g., Gogel, 1965; Erkelens & Collewijn, 1985; Regan, Erkelens, & Collewijn, 1986). Therefore, the difficulty in judging the absolute direction of a stimulus far away from the face is not an isolated perceptual phenomenon.

Given the high sensitivity to relative direction, the visual system can provide precise information about where an object is located with respect to its background or with respect to another stimulus. This information is useful when elements in the background or the other stimulus are already localized. Although the processed absolute direction may be imprecise when compared to relative direction, the absolute direction of a stimulus in the manual work space is necessary for action (e.g., reaching response). This speculation may come close to what underlies Erkelens and van Ee (in press) idea that the cyclopean eye is for action and irrelevant for visual direction, if by visual direction they mean relative visual direction.

Finally, to understand better the concept of the cyclopean eye, a point sometimes made but not emphasized (see Ono (1979)) is noted here to conclude this paper. The cyclopean illusion and the time-honored demonstrations listed in Experiment 1 require the concept of the cyclopean eye to explain them. When these observations are summarized as "Objects situated in the optic axis (i.e., *visual axis*), do not appear to be in that line, but in the common axis" (Wells, 1792, p. 46; italics ours), however, the implication of how the visual system and the oculomotor system work together to process direction from the cyclopean eye is not made explicit. Whenever the two eyes move to an object of interest, the common axis moves. This movement brings the common axis to pass through the object and the object is seen in the correct direction from the cyclopean eye. The illusion of seeing another object on the visual axis in an incorrect location is an epi-phenomenon for the two systems, oculomotor and visual, that evolved together to process correctly the direction of a binocularly fixated object. It is reasonable to conjecture that the two systems did not evolve to allow us to locate non-fixated stimuli or to make a line that points to an eye appear to point to the bridge of the nose. This epi-phenomenon, however, indicates to visual scientists that a binocularly or monocularly viewed object is seen from the cyclopean eye, and that the retinal location(s) of the stimulus and the joint eye positions together determine the absolute visual direction. The illusion that continues to hit you right between the eyes is a good example of the adage that "Illusions of the senses tell us the truth about perception."—"das Sinnestäuschungen Gesichtwahrheiten sind." (a quote attributed to Purkinje by Teuber (1960, p. 1602)).

Acknowledgements

This research was supported by grant A0296 from the Natural Sciences and Engineering Research Council of Canada (H.O.), the York University Faculty of Arts Research Fund (H.O.), and a York University Contract Faculty Research Grant (A.P.M.). The eye movements were recorded at the Oculomotor Laboratory of the Vision Science Research Program of the University Health Network (Director: Dr. M. J. Steinbach) and were supported by the Sir Jules Thorn Charitable Trust.

The authors wish to thank O. Espiritu and L. Lillakas for their help in collecting and analyzing data, and editing the paper, and M. Banks, E. Brenner, J. T. Enright, E. Gonzalez, P. Grove, R. Kohly, R. Ono, K. Phillips, D. M. Regan, and M. J. Steinbach for their helpful comments and discussions on an earlier version of this paper. We also like to thank A. Howard for translating Holland (1958) into English, and R. Blake for suggesting and arranging this paper to appear back to back with Erkelens and van Ee (in press).

Appendix A

We present sample version traces of four observers in Fig. 8, and the mean magnitudes of each sub-condition of each observer in Table 3. (The mean peak velocities were not included to shorten the appendix.) The traces reported in Fig. 8 are meant to supplement those shown in Erkelens (2000) and include traces he did not report (i.e., those from the dark condition). These traces mirror what is reported in Table 3. The traces and mean values show that the version eye movements, in both the tracking and stepping conditions, were smaller with monocular viewing than with binocular viewing. They also show the differences between the bright and dark conditions: the dark condition produced smaller version eye movements than the bright condition. However, the association between who experienced the cyclopean illusion and the magnitude of the eye movement in the monocular dark condition was not perfect. Comments on the individual eye movements follow.

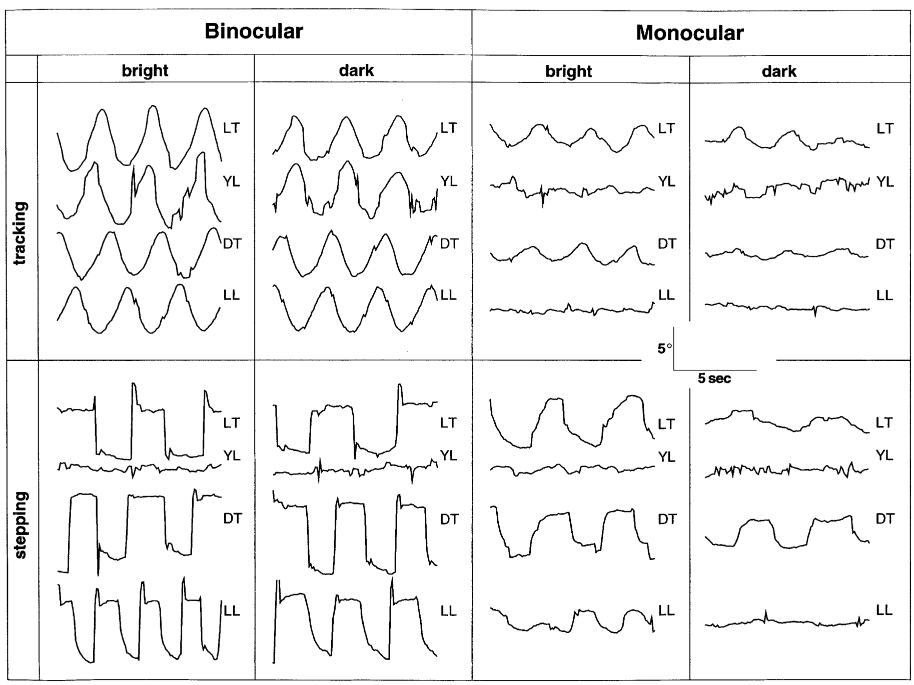

Fig. 8. Sample version traces from each condition for the four observers who participated in the eye-movement monitoring session in Experiment 2.

Table 3
Mean magnitudes (standard deviations) of the version component of each observer's eye movements in the binocular and monocular viewing conditions (in degrees)

Observers	Binocular		Monocular	
	Bright	Dark	Bright	Dark
Tracking magnitude				
LT	4.95 (0.44)	4.85 (0.37)	2.46 (0.55)	1.20 (0.52)
YL	5.25 (1.83)	3.59 (2.00)	1.19 (0.49)	1.18 (0.46)
DT	5.14 (0.31)	4.69 (0.34)	2.17 (0.56)	1.18 (0.44)
LL	5.67 (0.42)	5.03 (0.23)	0.76 (0.39)	0.00 (0.00)
Stepping magnitude				
LT	6.89 (1.29)	6.82 (1.17)	4.93 (0.63)	2.14 (0.85)
YL				
DT	7.81 (1.47)	7.45 (0.97)	4.40 (1.12)	3.34 (0.52)
LL	7.11 (1.47)	6.70 (1.17)	1.70 (0.91)	0.60 (0.30)

A.1. Observers LT's, YL's and DT's eye movements

Although two of these observers LT and YL experienced the cyclopean illusion, they did not have the largest eye movements in the dark conditions. (Observer DT, who did not experience the illusion, had the largest eye movement in the dark/stepping condition.) This lack of a perfect association suggests that the magnitude of the version eye movement is not the sole determinant for experiencing the illusion in the dark condition.

Observer YL was unable to move her eyes as requested in the stepping condition (see sample data). In the tracking condition, however, she was able to track the moving stimulus, albeit not as well as did Observer LT. Her ability to track and inability to step is consistent with her experiencing the cyclopean illusion in the tracking condition, but not in the stepping condition.

A.2. Observer LL's and Erkelens' eye movements

In the dark/monocular condition, Observer LL was unable to move her eyes in the tracking condition, which is consistent with her not experiencing the cyclopean illusion, as well as her large exophoria for the stimulus at 15 cm. She was the oldest observer (age 43) comparable in age with Erkelens (48), and her reduced accommodative range was expected. In the bright/monocular condition, the movement of Erkelens' eyes (reported in Erkelens (2000)) and the movement of Observer LL's eyes (reported here) were likely due to their ability to use the isotropic rate of change in retinal image size of the stimulus holder. It is likely that Erkelens' eye movements (or lack thereof) in the dark/monocular condition would be similar to those of Observer LL, because the accommodative stimuli in his experiment were closer than his reported accommodative near point of 30 cm.

Addendum

In response to Erkelens and van Ee (in press) addendum, we reiterate and briefly elaborate on a few key points made in our paper. In the spirit suggested by the action editor, R. Blake, we offer constructive suggestions as to how to resolve the outstanding issues.

For Experiment 1, the empirical question remains as follows: Where do observers perceive stimuli physically positioned on the visual axis of one eye, when the other eye is occluded? Do the stimuli appear in their veridical locations (i.e., on the visual axis), as claimed by Erkelens (2000) and Erkelens and van Ee (in press) or do they appear in illusory locations (i.e., on the common axis) as claimed by us? Our results complimented what has been reported in the literature for over two millennia; namely, the stimuli appeared on the common axis. Since the question involves the perceived locations of the stimuli rather than the observers' knowledge of the physical locations of the stimuli, observers were asked to report their percept. Erkelens and van Ee suggest that this procedure does not meet today's psychophysical standards. We had assumed, reasonably we think, that the known location conflicted with the perceived location. An alternative procedure would be to prevent observers from having any access to information about the stimuli's actual locations. In the spirit of trying to resolve this issue to their satisfaction, we are willing to design and conduct such an experiment with them; we are confident that our results will be confirmed. Moreover, their concern about observers coming off the biteboard to make their responses is not germane to the empirical question. The question is concerned with the accuracy (constant error) of the reports, not the precision (variable error). Thus, a case cannot be made that "a translation of the head of ± 1 mm" caused the stimuli to be perceived on the common axis (in front of the nose) instead of on the visual axis (in front of the eye). Also, any translation of the head upon returning to the biteboard would have resulted in a shift in the relative direction of the stimuli; no such shift was reported by any of our 12 observers.

For Experiment 2, their critique is based on an incorrect assumption. We did not argue, as they suggest, that the sole determinant of the cyclopean illusion is the magnitude of the eye movement. We hypothesized that information about the relative direction of the stimuli with respect to the background can, in certain stimulus situations, "override" information about absolute direction, and thus affect the occurrence of the illusion. Without this hypothesis Erkelens (2000) himself cannot account for the results of the four observers who experienced the illusion under his monocular viewing condition. His results falsify ("one would have sufficed" to use Erkelens and van Ee (in press) term) his hypothesis that perceived direction during monocular viewing is based on signals from only one eye. Moreover, the imaginary line that points to the nose and "pivots" very near or at the face is a description of the cyclopean illusion (see Fig. 1). Erkelens and van Ee attribute this pivoting to a "misalignment between the stimuli and the viewing eye". If, as they argue, perceived direction during monocular viewing is based on signals of the viewing eye only, then no such pivoting (change in absolute direction) should occur. This holds true irrespective of whether the stimuli are aligned or not. The only way such pivoting can occur is if the signals of both eyes are used. In any event, in the spirit of resolving this issue, we are willing to share with them, or any other interested readers, the eye movement data from our observers' individual eyes.

Finally, we note that no explicit distinction between relative and absolute direction was made in either Wells (1792), in Hering (1879/1942), or in what Ono and Mapp (1995) called Wells–Hering's laws of visual direction. We now have a schematic input–output representation of a direction mechanism that combines Wells and Hering's thinking and this important distinction. Readers are referred to Ono, Lillakas, and Mapp (in press) to examine this combination as well as a further discussion on the relevance of the concept of the cyclopean eye.

References

Aggarwala, K. R., Nowbotsing, S., & Kruger, P. B. (1995). Accommodation to monochromatic and white targets. *Investigative Ophthalmology and Vision Science, 36*, 2695–2705.

Alhazen, I. (1083/1989). *Book of optics*. In *The optics of Ibn al–haytham two volumes*. (A. I. Sabra, Trans.) London: Warburg Institute (originally published 1083).

Alpern, M., & Ellen, P. (1956). A quantitative analysis of the horizontal movements of the eyes in the experiment of Johannes Mueller—I. Methods and results. *American Journal of Ophthalmology, 42*, 289–296.

Banks, M. S., van Ee, R., & Backus, B. T. (1997). The computation of binocular visual direction: a re-examination of Mansfield and Legge (1996). *Vision Research, 37*, 1605–1610.

Barbeito, R. (1981). Sighting dominance: an explanation based on the processing of visual direction in the tests of sighting dominance. *Vision Research, 21*, 855–860.

Barbeito, R., & Ono, H. (1979). Four methods of locating the egocenter: a comparison of their predictive validities and reliabilities. *Behavior Research Methods and Instrumentation, 11*, 31–36.

Barbeito, R., & Simpson, T. L. (1991). The relationship between eye position and egocentric visual direction. *Perception and Psychophysics, 50*, 373–382.

Blake, R., & Cormack, R. H. (1979). On utrocular discrimination. *Perception and Psychophysics, 26*, 53–68.

Brenner, E., & Cornelissen, F. W. (2000). Separate simultaneous processing of egocentric and relative positions. *Vision Research, 40*, 2557–2563.

Bridgman, P. W. (1927). *The logic of modern physics*. New York: Crowell-Collier-Macmillan.

Carpenter, R. H. S. (1988). *Movement of the eyes*. Pion: London.

Cline, D., Hofstetter, H. W., & Griffin, J. R. (Eds.). (1989). *Dictionary of visual science* (4th ed.). Radnor, Pennsylvania: Chilton Trade Book Publishing.

Cumming, B. G., & Judge, S. J. (1986). Disparity-induced and blur-induced convergence eye movement and accommodation in monkey. *Journal of Neurophysiology, 55*, 896–914.

Davies, P. (1973). Effects of movements on the appearance and duration of a prolong visual after image. *Perception, 2*, 147–153.

DiScenna, A. O., Das, V., Zivotofsky, A. Z., Seidman, S. H., & Leigh, R. J. (1995). Evaluation of a video tracking device for measurement of horizontal and vertical eye rotations during locomotion. *Journal of Neuroscience Methods, 58*, 89–94.

Duncker, K. (1929/1935). Über induzierte Bewegung (Ein Beitrag zur Theorie optisch wahrgenommener Bewegung). *Psychologische Forschung, 12*, 180–259. Abridged and translated as "Induced motion". In W. D. Ellis (Ed. and Trans.). *Source book of gestalt psychology* (pp. 161–172). London: Routledge and Kegan Paul.

Enright, J. T. (1988). The cyclopean eye and its implications: vergence state and visual direction. *Vision Research, 28*, 925–930.

Enright, J. T. (1992). The remarkable saccades of asymmetrical vergence. *Vision Research, 32*, 2261–2276.

Erkelens, C. J. (2000). Perceived direction during monocular viewing is based on signals of the viewing eye only. *Vision Research, 40*(18), 2411–2419.

Erkelens, C. J., & Collewijn, H. (1985). Motion perception during dichoptic viewing of moving random-dot stereograms. *Vision Research, 25*, 583–588.

Erkelens, C. J., & Regan, D. (1986). Human ocular vergence movements induced by changing size and disparity. *Journal of Physiology, 379*, 145–169.

Erkelens, C. J., Muijs, A. J. M., & van Ee, R. (1996). Binocular alignment in different depth planes. *Vision Research, 36*, 2141–2147.

Erkelens, C. J., & van Ee, R. (1997). Capture of the visual direction of monocular objects by adjacent binocular objects. *Vision Research, 37*, 1735–1745.

Erkelens, C. J., & van Ee, R. (in press). The role of the cyclopean eye in vision: sometimes inappropriate, always irrelevant. *Vision Research, 42*, 1157–1163.

Feigl, H. (1945). Operationism and scientific method. *Psychological Review, 52*, 250–259.

Gogel, W. C. (1965). Equidistance tendency and its consequences. *Psychological Bulletin, 64*, 153–163.

Gray, R., & Regan, D. (1998). Accuracy of estimating time to collision based on binocular and monocular information. *Vision Research, 38*, 499–512.

Green, C. D. (1992). Of immortal mythological beasts: operationism in psychology. *Theory and Psychology, 2*, 291–320.

Helmholtz, H. (1910/1962). In J. P. C. Southall (Ed.). *Helmholtz's treatise on physiological optics. Vol. 3*. (3rd German ed. and Trans.). New York: Dover. (Originally published 1910).

Hering, E. (1879/1942). *Spatial sense and movements of the eye* (C. A. Radde, Trans.). Baltimore: American Academy of Optometry. (Originally published 1879).

Hering, E. (1868/1977). In B. Bridgeman, & L. Stark (Eds.). *The theory of binocular vision* (B. Bridgeman, Trans.). New York: Plenum Press. (Original work published 1868).

Hermann, J. S., & Samson, C. R. (1967). Critical detection of the accommodative convergence to accommodation ration by oculography. *Archives of Opthalmology, 78*, 424–430.

Holland, G. (1958). Untersuchung über den Einfluss der Fixationsentfernung und der Blickrichtung auf die horizontale Heterophorie (Exo- und Esophorie). *v. Graefes Archiv für Opthalmologie, 160*, 144–160.

Howard, I. P. (1982). *Human visual orientation*. Chichester: Wiley.

Howard, I. P. (1991). Spatial vision within egocentric and exocentric frames of reference. In S. R. Ellis (Ed.). *Pictorial communication in virtual and real environment*. New York: Taylor and Francis.

Howard, I. P. (1996). Alhazen's neglected discoveries of visual phenomena. *Perception, 25*, 1203–1217.

Howard, I. P., & Rogers, B. (1995). *Binocular vision and stereopsis*. Oxford: Oxford University Press.

Howard, I. P., & Templeton, W. B. (1966). *Human spatial orientation*. London: Wiley.

Howard, I. P., & Wade, N. J. (1996). Ptolemy's contributions to the geometry of binocular vision. *Perception, 25*, 1189–1201.

Ittelson, W. H. (1951). Size as a cue to distance; radial motion. *American Journal of Psychology, 64*, 188–202.

Keller, E. L., & Robinson, D. A. (1972). Abducens unit behavior in the monkey during vergence eye movements. *Vision Research, 12*, 369–382.

Kenyon, R. V., Ciuffreda, K. J., & Stark, L. (1978). Binocular eye movements during accommodative vergence. *Vision Research, 18*, 545–555.

Leibowitz, H. (1955). Effect of reference lines on the discrimination of movement. *Journal of the Optical Society of America, A2*, 829–830.

Mapp, A. P., & Ono, H. (1999). Wondering about the wandering cyclopean eye. *Vision Research, 39*(14), 2381–2386.

Mitson, L., Ono, H., & Barbeito, R. (1976). Three methods of measuring the location of the egocentre: their reliability, comparative locations and intercorrelations. *Canadian Journal of Psychology, 30*, 1–8.

Ohtsuka, S., & Ono, H. (1998). Adjustment for displacement and compression triggered by pictorial cue of occlusion produces correct 3-D perception and Kanizsa's illusion. *Investigative Ophthalmology and Vision Science, 39*, S850.

Ono, H. (1979). Axiomatic summary and deductions from Hering's principles of visual direction. *Perception and Psychophysics, 25*, 473–477.

Ono, H. (1980). Hering's law of equal innervation and vergence eye movement. *American Journal of Optometry and Physiological Optics, 57*, 578–585.

Ono, H. (1983). The combination of version and vergence. In C. M. Schor, & K. J. Ciuffreda (Eds.). *Vergence eye movements: basic and clinical aspects* (pp. 373–400). Toronto: Butterworth.

Ono, H. (1991). Binocular visual directions of an object when seen as single or double. In D. Regan (Ed.). *Vision and visual dysfunction, Vol. 9 Binocular vision* (pp. 1–18). New York: MacMillan.

Ono, H., & Angus, R. G. (1974). Adaptation of sensory-motor conflict produced by the visual direction of the hand specified from the cyclopean eye. *Journal of Experimental Psychology, 103*, 1–9.

Ono, H., & Barbeito, R. (1982). The cyclopean eye vs the sighting dominant eye as the center of visual direction. *Perception and Psychophysics, 32*, 201–210.

Ono, H., & Barbeito, R. (1985). Utrocular discrimination is not sufficient for utrocular identification. *Vision Research, 25*, 289–299.

Ono, H., & Gonda, G. (1978). Apparent movement, eye movement and phoria when two eyes alternate in viewing a stimulus. *Perception 7*, 75–83. Also reprinted in Rock, I. (1997) (Ed.). *Indirect perception* [*Title changed to: Apparent motion based on changing phoria*] (pp. 265–276). Cambridge: MIT Press.

Ono, H., Lillakas, L., & Mapp, A. P. (in press). The making of the direction sensing system for the Howard eggmobile. In L. Harris, & M. Jenkin (Eds.). *Levels of perception: a festschrift for Ian P. Howard*. New York: Springer.

Ono, H., & Mapp, A. P. (1995). A restatement and modification of Wells–Hering's laws of visual direction. *Perception, 24*, 237–252.

Ono, H., & Nakamizo, S. (1977). Saccadic eye movements during changes in fixation to stimuli at different distances. *Vision Research, 17*, 233–238.

Ono, H., & Nakamizo, S. (1978). Changing fixation in the transverse plane at eye level and Hering's law of equal innervation. *Vision Research, 18*, 511–519.

Ono, H., Nakamizo, S., & Steinbach, M. J. (1978). Non-additivity of vergence and saccadic eye movement. *Vision Research, 18*, 735–739.

Ono, H., Ohtsuka, S., & Lillakas, L. (1998). The visual system's solution to Leonardo da Vinci's paradox and to the problems created by the solution. *Proceeding for the workshop on visual cognition* (pp. 125–136).

Ono, H., Shimono, K., Saida, S., & Ujike, H. (2000). Transformation of the visual-line value in binocular vision: stimuli on corresponding points can be seen in two different directions. *Perception, 29*, 421–436.

Ono, H., Tam, W. J., & McConnell, S. (1983). Apparent displacement with a monocular prism differs from optical displacement. *Journal of Experimental Psychology: Human Perception and Performance, 9*, 652–656.

Ono, H., Wade, N. J., & Lillakas, L. (in press). The pursuit of leonardo's constraint. *Perception*.

Ono, H., & Weber, E. V. (1981). Nonveridical visual direction produced by monocular viewing. *Journal of Experimental Psychology: Human Perception and Performance, 7*, 937–947.

Ono, H., Wilkinson, A., Muter, P., & Mitson, L. (1972). Apparent movement and change in perceived location of a stimulus produced by a change in accommodative vergence. *Perception and Psychophysics, 12*, 187–192.

Owens, D. A., & Leibowitz, H. W. (1975). The fixation point as a stimulus for accommodation. *Vision Research, 15*, 1161–1163.

Owens, D. A., & Tyrrell, R. A. (1992). Lateral phoria of distance: contributions of accommodation. *Investigative Ophthalmology and Vision Science, 33*, 2733–2743.

Park, K., & Shebilske, W. L. (1991). Phoria, Hering's law and monocular perception of direction. *Journal of Experimental Psychology: Human Perception and Performance, 17*, 219–231.

Pelz, J. B., & Hayhoe, M. M. (1995). The role of exocentric reference frames in the perception of visual direction. *Vision Research, 35*, 2267–2275.

Popple, A. V., & Findlay, J. M. (1998). Is monocular alignment computed by binocular neurones? *Investigative Ophthalmology and Vision Science, 39*, S622.

Regan, D., & Beverley, K. I. (1978). Looming detectors in the human visual pathway. *Vision Research, 18*, 415–421.

Regan, D., Erkelens, C. J., & Collewijn, H. (1986). Necessary conditions for the perception of motion in depth. *Investigative Ophthalmology and Vision Science, 27*, 584–597.

Riggs, L. A., & Niehl, E. W. (1960). Eye movements recorded during convergence and divergence. *Journal of the Optical Society of America, 50*, 913–920.

Saida, S., Ono, H., & Mapp, A. P. (2001). Closed-loop and open-loop accommodative vergence eye movements. *Vision Research, 41*(1), 77–86.

Sheedy, J. E., & Fry, G. A. (1979). The perceived direction of the binocular image. *Vision Research, 19*, 201–211.

Shimono, K., Ono, H., Saida, S., & Mapp, A. P. (1998). Methodological caveats for monitoring binocular eye position with nonius stimuli. *Vision Research, 38*, 591–600.

Snowden, R. J. (1992). Sensitivity to relative and absolute motion. *Perception, 21*, 563–568.

Steinbach, M. J., Howard, I. P., & Ono, H. (1985). Monocular asymmetries in vision: we don't see eye to eye. *Canadian Journal of Psychology, 39*, 476–478.

Sterken, Y., Postma, A., de Haan, E. H. F., & Dingemans, A. (1999). Egocentric and exocentric spatial judgements of visual displacement. *The Quarterly Journal of Experimental Psychology, 52A*(4), 1047–1055.

Stevens, S. S. (1935). The operational definition of psychological concepts. *Psychological Review, 42*, 517–527.

Swindle, P. F. (1916). Positive after-images of long duration. *American Journal of Psychology, 27*, 324–334.

Teuber, H. L. (1960). Perception. In J. Field (Ed.). *Handbook of physiology—Neurophysiology III (Chap. LXV)*. Baltimore: Williams & Wilkins.

van Ee, R., Banks, M. S., & Backus, B. T. (1999). Perceived visual direction near an occluder. *Vision Research, 39*, 4085–4097.

Wade, N. J., & Swanston, M. T. (1987). The representation of nonuniform motion: induced motion. *Perception, 16*, 555–571.

Welch, R.B. (1986). Adaptation of space perception. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.). *Handbook of perception and performance (Chapter 24)*. New York: Wiley.

Wells, W. C. (1792). *An essay upon single vision with two eyes: together with experiments and observations on several other subjects in optics*. London: Cadell.

Westheimer, G., & Mitchell, A. M. (1956). Eye movements responses to convergence stimuli. *Archives of Ophthalmology, 55*, 848–856.

Yarbus, A. L. (1967). *Eye movements and vision* (B. Haigh, & L. A. Riggs, Trans.). New York: Plenum Press. (Originally published, 1965).

Zenkin, G. M., & Petrov, A. P. (1979). On the constancy mechanisms for visual space perception. *Sensory systems [SENSORNYE SISTEMY]* (pp. 25–39). Leningrad: Nauka. This is a publication, which came out every year in Pavlov Institute of Physiology in Leningrad. We thank Dr. Nikolaev (Institute for Information Transmission Problems, Russian Academy of Sciences) for tracking down the paper and Dr. L. Kontsevich (Smith-Kettlewell Eye Research Institute) for translating the critical part of this paper into English. The translation is available by contacting the first author.